PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Ancillotto L, Amori G, Capizzi D, Cignini B, Zapparoli M, Mori E. 2024 No city for wetland species: habitat associations affect mammal persistence in urban areas. *Proc. R. Soc. B* **291**: 20240079. https://doi.org/10.1098/rspb.2024.0079

Received: 11 January 2024
Accepted: 9 February 2024

Subject Category:
Global change and conservation

Subject Areas:
ecology, environmental science

Keywords:
extinction, habitat, mammals, resampling, urban wildlife, wetlands

Author for correspondence:
Leonardo Ancillotto
e-mail: leonardo.ancillotto@cnr.it

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.7099106.

THE ROYAL SOCIETY PUBLISHING

Downloaded from https://royalsocietypublishing.org/ on 13 March 2024

No city for wetland species: habitat associations affect mammal persistence in urban areas

Leonardo Ancillotto[1,2], Giovanni Amori[1], Dario Capizzi[3], Bruno Cignini[4], Marzio Zapparoli[5] and Emiliano Mori[1,2]

[1]National Research Council (CNR), Institute for the Research on Terrestrial Ecosystems (IRET), via della Madonna del Piano 10, 50019 Sesto Fiorentino, Italy
[2]National Biodiversity Future Center (NBFC), Palermo, Italy
[3]Latium Region Directorate for Environment, Via di Campo Romano 65, 00173 Rome, Italy
[4]Department of Biology, University of Rome Tor Vergata, Rome, Italy
[5]Department for Innovation in Biological, Agro-food and Forest systems (DIBAF), Università degli Studi della Tuscia, via San Camillo de Lellis snc, 01100 Viterbo, Italy

LA, 0000-0002-8774-0671

The fast rate of replacement of natural areas by expanding cities is a key threat to wildlife worldwide. Many wild species occur in cities, yet little is known on the dynamics of urban wildlife assemblages due to species' extinction and colonization that may occur in response to the rapidly evolving conditions within urban areas. Namely, species' ability to spread within urban areas, besides habitat preferences, is likely to shape the fate of species once they occur in a city. Here we use a long-term dataset on mammals occurring in one of the largest and most ancient cities in Europe to assess whether and how spatial spread and association with specific habitats drive the probability of local extinction within cities. Our analysis included mammalian records dating between years 1832 and 2023, and revealed that local extinctions in urban areas are biased towards species associated with wetlands and that were naturally rare within the city. Besides highlighting the role of wetlands within urban areas for conserving wildlife, our work also highlights the importance of long-term biodiversity monitoring in highly dynamic habitats such as cities, as a key asset to better understand wildlife trends and thus foster more sustainable and biodiversity-friendly cities.

1. Introduction

Cities are expanding worldwide at fast rates [1,2], with increasing proportions of the global human population predicted to inhabit built-up environments in the near future [3,4]. Such an expansion largely implies the replacement of natural habitats with urban areas and their uniquely modified ecological conditions. The latter typically include, among many others, the spread of impervious surfaces, lack or scarcity of natural vegetation, several sources of air, water, soil, noise and light pollution [5], modified microclimatic conditions, and of course highest density of vehicles, humans and domestic animals [6]. Consequently, cities represent a challenging environment to wildlife living therein. Nonetheless, many wild species thrive in urban environments, with increasing amounts of scientific literature focusing on ecological processes that shape urban wildlife, such as the so-called urban filter, or on the micro-evolutionary paths that species undertake after becoming synurbic [7,8]. The success of species occurring in urban environments may though be the result of intrinsic species factors (e.g. ecological and biological traits) as well as extrinsic environmental ones (e.g. landscape structure and patterns of urban development) and casual (e.g. genetic stochastic processes). Such entangled mix of processes may lead to rapid changes in urban wildlife, i.e. by highly affecting time of persistence and spread of species within an area, as already evidenced for plants and birds in Mediterranean urban contexts (e.g. [9,10]).

© 2024 The Author(s) Published by the Royal Society. All rights reserved.

Downloaded from https://royalsocietypublishing.org/ on 13 March 2024

Recent studies agree in highlighting that wildlife extinction patterns in human-modified areas are not random, with a clear effect of traits mostly related to the ability of species to persist in highly fragmented landscapes [7], or to adapt to natural environments whose conditions somehow resemble those of anthropogenic habitats. As an example, Fraissinet *et al.* [10] found that forest-adapted birds seem to thrive in urban habitats, showing disproportionate increases in their local occupancy in recent times if compared with species associated with open habitats. This result, supported by similar examples across Europe, may probably stem from both the use of cavities—a key resource for breeding birds—that are highly available in urban areas, and the increase of wooded cover in both urban and non-urban areas in Europe [11].

Besides some clear patterns in species dynamics in cities, and a steep increase in the numbers of studies dealing with urban wildlife in the last decades [12], most literature on the topic is focused on few taxonomic groups [13], leaving huge gaps in our ability to understand, and possibly overcome, extinction processes in cities. Namely, a significant portion of current knowledge on urban wildlife derives from studies on birds and carnivores, and particularly on few species within the latter group (i.e. foxes and coyotes), with a scarcity of studies following multi-taxa approaches [13]. Mammals as a group offer a unique opportunity to test hypotheses on ecological dynamics in urban areas for several reasons. First, mammals are highly diversified both within and among different orders, in terms of e.g. size and ecology, which make them suitable to assess the effect of different factors in affecting their occurrence [14]. Moreover, most mammal groups, particularly in Europe, have a stable taxonomy and feature a clear and consistent biogeography, so that even ancient records may still be reasonably acceptable in terms of species assignment; as an example, among Italian mammals (counting *ca* 115 terrestrial species), few taxa have been described in recent times, and all show clearly distinct distributions with little to no overlap with sister species from which they have been split [15]. As a last point, there is a long-standing tradition of studies on mammals as a group, so many records are available dating back to decades ago [7], giving us the opportunity to test hypotheses on the long-term effects of habitat changes on these animals.

Here we use the city of Rome, Italy, and its mammalian fauna, as a model system to define patterns of local extinction and persistence within large urban areas, testing the hypothesis that association to different habitats may drive the fate of species at local level. Specifically, we build on the evidence that cities usually disproportionately replace natural habitats, reclaiming more often specific habitat types such as wetlands, in comparison with forested areas, due to their occurrence upon terrains more suitable to buildings (e.g. in terms of slope and soil conditions; [9]). More specifically, wetlands are particularly prone to be replaced by urban development of cities [16], despite maintaining a key role in sustaining biodiversity of e.g. birds, plants and invertebrates [17], even when very isolated or polluted. As such, we predict that species associated with these habitat types are more likely to disappear over time in comparison with those associated with other environments at lower risk of replacement.

2. Material and methods

(a) Study area

We conducted our study in the metropolitan area of Rome, central Italy, the largest Italian city and one of the most ancient urban areas in Europe, extending over 36 000 ha and hosting *ca* 3 million inhabitants (https://demo.istat.it/). The area is dominated by built-up surfaces comprising from sparse to very high-density districts, densely interspersed by a rich network of green areas ($N = 1798$) that cumulatively cover 17 300 ha and include natural, semi-natural, recreational and agricultural patches whose intended use is officially categorized as 'green space'. Between the years 1750 and 1870 the human population inhabiting Rome raised from approximately 150 000 to 200 000 [18], yet most of its urban development occurred after World War II, as for many cities across Europe, so that most of the land-use changes occurred between 1940 and 1960. A more recent phase of urban expansion occurred also in the 1980–1990 decade, consisting of mostly unauthorized or poorly regulated development. Between 1950 and 1990 the yearly rates of land reclamation in Rome ranged between 3 and 5%, dropping to less than 1% in the early 2000s [19]; the main changes consisted of the tripling of built-up surfaces, mainly at the expense of extensive agricultural areas, wetlands and woodlands, decreasing to *ca* 30, 50 and 60% of their original extent, respectively [19]. For this study, we considered the territory encompassed by the Great Ring Road (Grande Raccordo Anulare) as study area, as in other studies targeting Rome's wildlife and urban landscape [20–22]. Rome may be considered as an ideal setting to study urban mammals, thanks to a long tradition of natural history studies and large amounts of data available from its area (e.g. [23–27]). The mammalian assemblage in Rome features *ca* 40 species, according to the Atlas of Mammals of Rome project [24]: the most common and widespread mammals in the area are few highly adaptable species that thrive in anthropogenic landscapes (e.g. commensal rodents of genera *Rattus* and *Mus*, the red fox *Vulpes vulpes*, the common hedgehog *Erinaceus europaeus*, and the Kuhl's pipistrelle *Pipistrellus kuhlii*), yet species of conservation concern are also recorded (e.g. several bats listed in Annex II of the EU Habitats Directive). Three alien mammals occur in the urban area of Rome, deriving from ancient introduction events (the crested porcupine *Hystrix cristata*; [27]) and more recent ones (the Siberian chipmunk *Eutamias sibiricus*, and the coypu *Myocastor coypus*; [24,26]).

(b) Data collection

A systematic collection of records of mammals from the study area was conducted for the 'Atlas of Mammals of Rome' project in years 2008–2012; a record was considered as each observation of a mammal species within the study area at a given time. This campaign collated historical data from (i) a meticulous search of grey literature, monographs and historical sources, and (ii) inspection of local museum collections. These two approaches identified two main sources i.e. published and unpublished museum catalogues (Alessandrini 1985 (Catalogo metodico delle collezioni del Museo di Zoologia. Vertebrata. Mammalia. Unpublished manuscript, 7 pp.); [28]). Additional records were retrieved from (iii) Rome's Wildlife Rescue Centre run by LIPU, and (iv) systematic research in the field by trained operators. We completed data collection by retrieving recent records by (v) citizen science projects on the iNaturalist platform (project: 'Rome's mammals', https://www.inaturalist.org/projects/mammiferi-di-roma?test=apiv2) and (vi) recent literature (after year 2012), specifically by searching for '*Rome*' and '*Roma*' (in Italian) and '*mammals*' or either common and scientific names of mammals present in the region

Downloaded from https://royalsocietypublishing.org/ on 13 March 2024

[24] on Google Scholar and ISI Web of Science. Exact methods adopted for bibliographic and museum records are not available, while all field techniques applied in the targeted field sampling (iv) adhered to standardized protocols for e.g. acoustic sampling, live- and camera-trapping and visual tracking [29], and were performed at appropriate times of the year (e.g. summer months for bats, year-round for camera trapping, spring and autumn for live-trapping of small mammals).

We then assigned each retrieved record to one of four main source categories, i.e. bibliographic (including all records from either museum or published and grey literature), iNaturalist (all observations of wild species of mammals reaching the 'Research Grade' status deriving from the iNaturalist project 'Mammals of Rome', https://www.inaturalist.org/projects/mammiferi-di-roma/, accessed on 10 December 2023), rescue (all records of mammals admitted ad the Wildlife Rescue Centre of Rome, held by LIPU, the Italian partner of BirdLife International), and sampling (including all records obtained by targeted sampling conducted in the 2008–2012 campaign).

We also performed a taxonomic check of records in order to update species' identities according to split or nomenclatural changes, which resulted in minor corrections related to recent description of Italian endemic or sub-endemic species (e.g. from *Arvicola amphibius* to *A. italicus*, and from *Myotis nattereri* to *M. crypticus*; [15]).

We set the whole study area as even portions, by overlaying a 360 square grid (each square covering 1 km^2) on the city's map, in order to calculate the spatial spread of species across the study area in a standardized way. From the full record dataset, we only selected those fulfilling all the three following criteria: (i) identification at the species level, (ii) date of record available (at the year level), and (iii) exact coordinates or specific toponym associated with the record; for the last criterion, exact coordinates were clearly not available for older observations, and in those cases we only kept records when the reported toponym or notes allowed us to manually assign it to a specific 1×1 km grid cell. We also excluded a few records that probably consisted of accidentally translocated individuals or escapees from captivity.

We then organized data into three checklists, corresponding to the three main time frames describing the urban development history of Rome, and namely dividing records as (i) before 1950, (ii) between 1951 and 1990, and (iii) after 1990. This subdivision fits well with the two main waves of development that occurred in the city and that possibly affected species' persistence, e.g. immediately after World War II, relatively more recent urban expansion (ending in the 1990s), and current days.

For each species featured in the final dataset, we measured four spatio-temporal indicators of occurrence, in order to describe its spatial spread and trend within the study area through time i.e. (i) total cumulative numbers of records, (ii) time elapsed (in years) between first and last records, (iii) maximum past spatial spread, expressed as the number of square grid cells occupied until 1990, and (iv) apparent local extinction (no record after 1990). For the latter, we selected the year 1990 since the last systematic campaign to collect original data on mammals in the study area ended *ca* 25 years after that, i.e. species not recorded at least once in that period are likely to have genuinely disappeared from the area. We assigned each recorded species to a preferred habitat type, according to the available literature on Italian populations, i.e. associated with either forest, grassland or wetland; species specialized on any habitat types or associated with urban areas—such as commensal rodents—were classified as generalists; habitat assignments and related references are reported in the electronic supplementary material, file S1.

(c) Statistical analyses

In order to assess the potential effect of species' habitat preferences and spatial spread upon the risk of extinction, we built a generalized linear mixed model (GLMM), using habitat type (categorical, with four classes), time (categorical, corresponding to the three time frames considered), and their interaction term as explaining variables, adding species' past spatial spread as a covariate (fixed effects). We included taxonomic order as a random effect to take into account potential intra-class variability. We used apparent extinction (i.e. a '0' value at the more recent checklist) as a response variable, adopting a binomial error structure. Model fit to data was assessed by inspecting conditional and marginal *R*-squared values; i.e. considering either fixed effects only or both fixed and random effects, respectively. We considered significant those effects with $p < 0.05$ and confidence intervals of estimate not encompassing 0. Model was built in R [30], using the *lme4* package [31], and evaluated using the *DHARMa* [32] and *MuMIn* [33] packages.

3. Results

We retrieved 6342 records of mammals from the urban area of Rome, belonging to 51 species from six orders, and spanning in time from 1832 to 2023. The most frequently recorded species was the common hedgehog (*Erinaceus europaeus*) ($N = 2748$), followed by Savi's (*Hypsugo savii*) and Kuhl's pipistrelles (*Pipistrellus kuhlii*) ($N = 1321$ and 967, respectively), and by the red fox (*Vulpes vulpes*) ($N = 541$). Spatial spread of species changed significantly in time according to habitat preferences (figures 1 and 2*a*), with wetland-associated species showing decreasing or unclear patterns from 1950 to 2023. Namely, all wetland species either remained stable or decreased, with the exception of the introduced coypu (*M. coypus*), which showed a steep increase in its spatial spread in the last decades. Despite huge differences in the total numbers of records obtained per time interval (269, 841 and 5232 for 1950, 1990 and 2023 checklists, respectively), and the different main data sources for each checklist (figure 1*b*), species richness remained relatively stable in time (with 41, 41 and 42 species detected, respectively). Nonetheless, the numbers of species associated with different habitats changed between the first and last checklist, with a decrease in those associated with wetlands (from nine to four species) and an increase of generalists and forest species (from 17 to 20, and from 12 to 15, respectively; figure 1*c*).

Species' spread per time interval ranged between $N = 1$ (e.g. *Lutra lutra*, *Capreolus capreolus*, *Pipistrellus nathusii* and *Vespertilio murinus*) and $N = 218$ (*E. europaeus*). Most species recorded are habitat generalists ($N = 21$), yet several specialists are also present (forest: $N = 15$; wetlands: $N = 9$; grasslands: $N = 6$). Nine out of 51 species (17.6%) known to occur in the area have not been detected since 1990, and may thus be considered as locally (apparently) extinct, namely five bats, two rodents and two carnivores (figure 2*b*). Overall trends of spatial spread were relatively consistent across taxonomic orders from the first to the most recent checklist, with few exceptions: namely Chiroptera ranked first in terms of mean spatial spread in 1950, closely followed by Carnivora; conversely, the same two orders ranked as the last ones in 2023, with small terrestrial mammals (Rodentia, Eulipotyphla and Lagomorpha) being the most spread ones, on average (figure 2*a*).

Our model proved relatively fitting to our data (see residuals plotted in electronic supplementary material, figure S1) in explaining species' spread and probability of extinction of mammals in the study area (marginal $R^2 = 0.34$), and revealed a significant effect of species' preferred habitat type (estimate: 2.16 ± 1.01, $p = 0.002$). Namely, species associated with wetlands showed significantly

royalsocietypublishing.org/journal/rspb Proc. R. Soc. B 291: 20240079

Downloaded from https://royalsocietypublishing.org/ on 13 March 2024

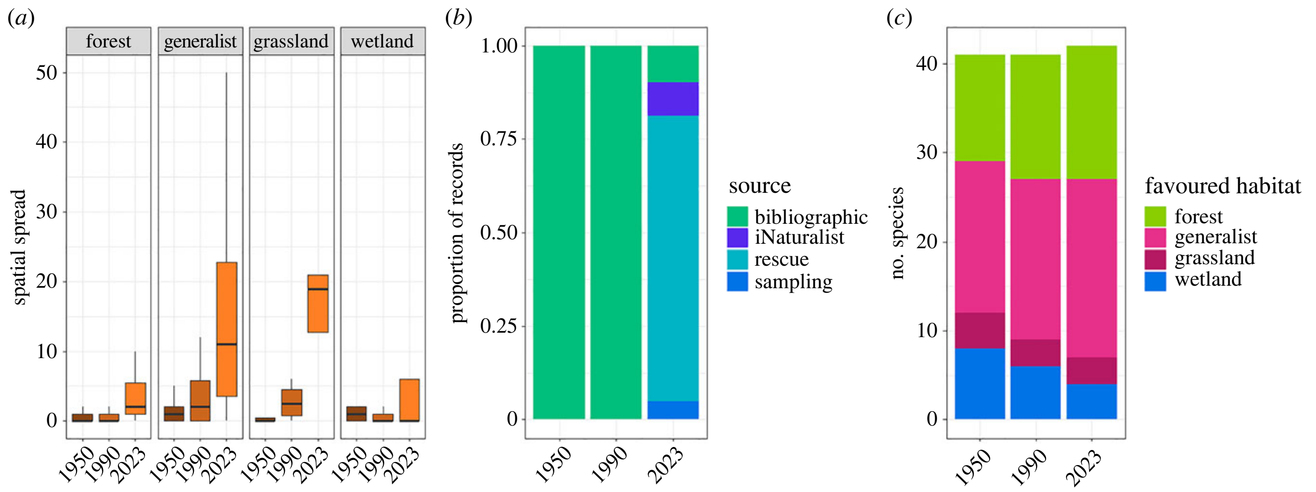

Figure 1. (*a*) Mean species' spatial spread (expressed as numbers of occupied 1 × 1 km square grid cells) of mammals in the city of Rome at three time intervals; (*b*) proportions of mammal records at each time interval according to different sources: bibliographic = record from literature or museum specimens; iNaturalist = record retrieved from the inaturalist.org citizen science platform; rescue = record from Rome's Wildlife Rescue Centre; sampling = record from targeted field sampling for the Atlas of Mammals of Rome project (unpublished); (*c*) numbers of species occurring in Rome at each time interval, according to their preferred habitat.

Figure 2. Mean spatial species' spatial spread (numbers of 1 × 1 km square grid cells) of occurrence of mammal species ($N = 51$) occurring in Rome, Italy, between years 1832 and 2023 (*a*); temporal span (in years) of species occurrence in the study area, separately according to species' preferred habitat type (*b*): brown = generalist; dark green = forests; light green = grasslands; light blue = wetlands. Species last recorded prior to 1990 (indicated by vertical dashed line) were considered as locally extinct in the last time interval. Outliers (entries out of the 95% confidence interval) not depicted.

higher probability of extinction in the last approximately 190 years, when compared with species associated with all other habitat types. In fact, 50% of the species considered as possibly extinct within the study area are associated with wetlands, while only two species associated with forests, one with grasslands, and one generalist apparently went extinct (figure 3). Conversely, species' past spatial spread did not explain a significant portion of model variance, despite having a marginal negative effect on species' probability of

Downloaded from https://royalsocietypublishing.org/ on 13 March 2024

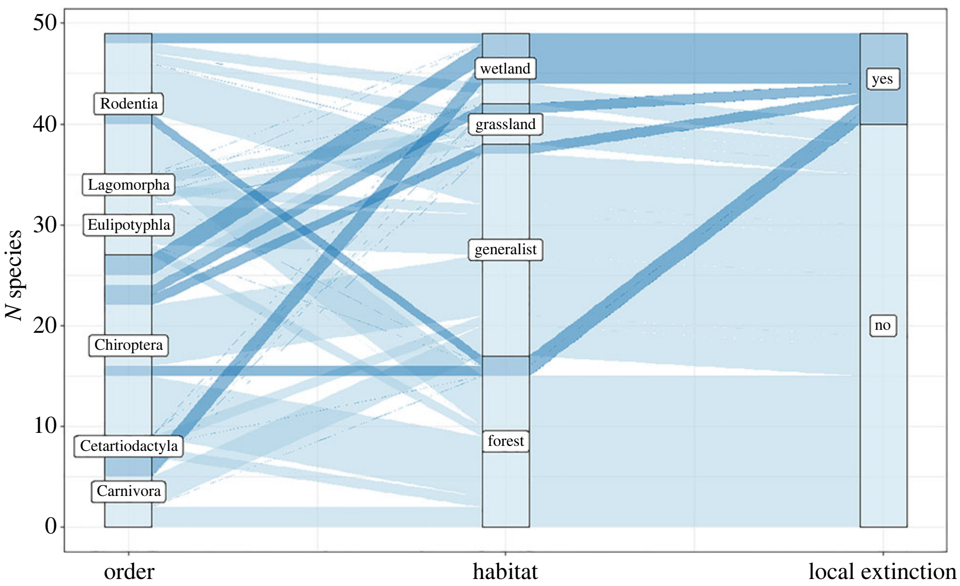

Figure 3. Alluvial plot depicting the numbers of mammal species that went locally extinct in the urban area of Rome between 1832 and 2023, according to taxonomic order and preferred habitat type.

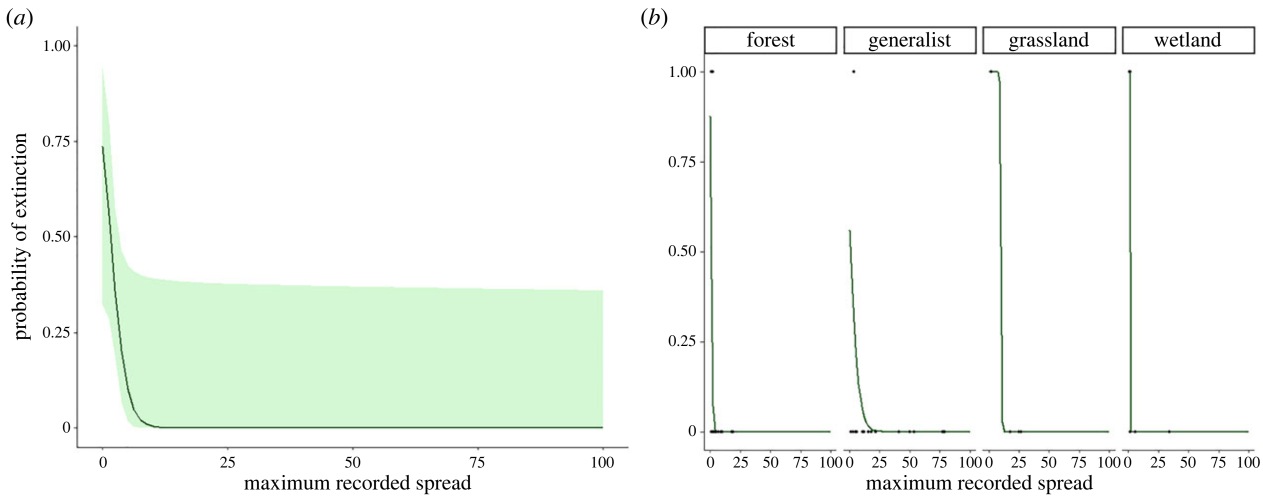

Figure 4. Probability of local mammal extinction as a function of maximum spatial spread (quantified as numbers of 1 × 1 square km grid cells) in the city of Rome between 1832 and 2023 according to generalized linear models on (*a*) all species ($N = 51$) and (*b*) separately for species preferring different habitat types (sample sizes: forest = 17, generalist = 22, grassland = 4, wetland = 9). Shaded area in (*a*) indicates 95% confidence interval.

extinction (estimate: −0.54 ± 0.50, $p = 0.06$; figure 4). In both models, taxonomic order as a random factor provided little to no additional contribution to the explained variance (delta value of conditional $R^2 < 0.01$).

4. Discussion

Understanding extinction in human-modified environments is key to protecting wildlife, particularly in the Anthropocene and its associated spread of urban areas worldwide, replacing natural habitats and threatening wildlife populations [34]. Here we documented greater than 150 years of mammal records from one of the most ancient urban areas of Europe, disclosing that Rome hosts relatively high numbers of species of mammals that have changed in time. Several species have in fact gone locally extinct within the urban area of Rome in the last decades, with such disappearance being disproportionately likely to involve species associated with wetlands. Wetlands are well-known biodiversity hotspots severely affected by anthropogenic pressures such as reclamation, drainage for agriculture, chemical pollution and climate change, all factors that decrease the quality and extent of these fragile ecosystems [16,35]. Consequently, many species strongly dependent upon wetlands, ranging from temporary pools to large riverine systems, are threatened and considered as important conservation targets [36].

In our specific case, several species apparently gone extinct are mostly bats that, despite their obvious higher dispersal abilities, were strongly dependent upon specific habitat structures or spatially limited habitats, such as underground roosts that were destroyed due to land reclamation for urban development. More specifically, this process in Rome led to the disappearance of large colonies of threatened species such as *Rhinolophus euryale*, *Miniopterus schreibersii* and *Myotis capaccinii*, all considered as declining and listed within the Annex II of the Habitats Directive. The same above-mentioned species are also associated with high-quality wetlands

Downloaded from https://royalsocietypublishing.org/ on 13 March 2024

(despite only *M. capaccinii* being strictly dependent upon wetlands; [37,38]), thus probably representing a case of synergistic factors affecting species' persistence in urban areas. Land reclamation for urban development, and impoverishment of quality of water sites such as, in our case study, the Tevere and Aniene rivers, well known to have decreased in their ecological conditions [39,40] in the last decades, may both have played a role in the local extinction of these species. The same decrease of water quality, associated with the heavy modifications of riverbanks, whose vegetation has been largely removed, may have caused the disappearance of wetland-associated mammals from other orders as well, i.e. the Italian water vole (*A. italicus*), the Eurasian otter (*Lutra lutra*) and the western polecat (*Mustela putorius*), all recorded for the last time before 1950 (e.g. [41]). Interestingly, historical wetlands where water-associated species went locally extinct are actually still present in the area, being represented by sections of the two larger rivers and artificial basins; nonetheless, Roman wetlands strongly decreased during the last urban development wave of the city [19]. As such, our results highlight how land reclamation and habitat replacement in urban areas are not necessarily the only processes underlying the extinction of species associated with wetlands, as other aspects such as pollution, landscape connectivity or direct disturbance may play a relevant—synergistic—role on a wider spatial scale [42].

Our approach clearly presents potential biases, e.g. in terms of data sources; more specifically, sampling efforts could not be assessed, especially for observations coming from historical records, and may strongly differ among sources. Nonetheless, we adopted a cautious approach by (i) only considering species as apparently and locally extinct, i.e. not excluding that a species classified as extinct was actually still present—albeit with very low densities or at undisclosed sites—and (ii) not taking into account potential or actual colonization by new species (which would have required a more balanced sampling effort through time). Moreover, sampling effort in terms of numbers of records per time interval steeply increased in time within our study area, further suggesting that our data may be actually biased against apparent extinctions, and not vice versa [25]. Any potential habitat-based bias, due to e.g. difficulties in locating and sampling wetland sites, may also be excluded in our case study, since the more recent time frame included targeted sampling covering the entire city, thus providing an updated and exhaustive picture of current mammalian diversity occurring in the area, as also suggested by the discovery of at least two species associated with wetlands and unnoticed in previous campaigns (i.e. *P. pygmaeus* and *Myotis daubentonii*). Moreover, such a wide time interval presents some inevitable unevenness in the taxonomy considered. For instance, including some recently identified species may not represent an actual increase in species richness, but simply reflect improvement in taxonomic knowledge. This is, for example, the case for *P. pygmaeus*, a species only recently separated from *P. pipistrellus* [43]. Therefore, historical records may refer to either species [15].

Species' trends inside urban areas may also reflect general trends at wider spatial scales, e.g. region of country, and not necessarily be due to factors strictly related to the urban area itself. As an example, a few locally extinct mammals in Rome also experienced dramatic declines across their Italian and/or European ranges. Among these, the garden dormouse (*Eliomys quercinus*) and the grey long-eared bat (*Plecotus austriacus*) are typical examples of species whose conservation status and extinction risk, according to the Habitats Directive reporting and IUCN Red List, respectively, have worsened in the last assessments [44,45]. In our study area, these two species, usually associated with extensive mosaic landscapes of semi-open habitats and traditional farming [44,46], were both naturally rare when first recorded (two sites only). Consequently, the great wave of urban development and the associated landscape changes that occurred in Rome and its surroundings in the second half of the twentieth century may have wiped out these sensitive species earlier than the time frame we considered, a process likely to have occurred widely across their entire ranges.

Several sets of traits influence the ability of wildlife to persist and thrive in urban environments [47]. For mammals, key roles in influencing synurbization are played by reproduction-related traits such as litter size, as well as niche generalism, behavioural and cognitive plasticity, and spatial ranging abilities [7], all considered as functional to cope with the higher mortality rates and lower ecological connectivity conditions, typical of urban environments. Yet, we still know little on the role of habitat preferences in mammal adaptation to urban environments. Conversely, several studies on birds disclose that habitat-related traits such as nesting substrate or preferred habitat type deeply influence the probability of species to thrive in cities around the world [10,48,49]. As an example, bird species naturally associated with forest and rocky/cliff habitats are usually the 'winners' when urbanization occurs, a phenomenon consistent across biomes and geographical regions [50,51].

The unusually high richness ($N = 51$) of Rome's mammal assemblage is unmatched by any other European city for which data on mammals are available, with Warsaw, Berlin, Moscow and Lodz all ranging between 35 and 46 species [52]. Such high diversity is probably due to the complex landscape configuration of the city, comprising wide semi-natural and protected areas even in close proximity of the city centre. All these elements provide space to natural vegetation remnants within the urban matrix (as in [9]) and, consequently, shelter to wild species from many taxonomic groups [22,53], including mammals (e.g. [21,27]). Our work highlights the important role of habitat preferences in predicting species' trends in modified habitats [54], a key asset for the conservation of threatened species, and the development of wildlife-friendly and sustainable cities in the future. Moreover, we disclose that—despite relatively significant changes in species' occurrences in time—cities may host diverse mammalian communities (as in [55]), and represent important strongholds for endangered and protected species. The species' turnover we detected also suggests that time-series analyses may reveal how trait-based filtering of species due to urbanization may occur at least at two functional and temporal scales, i.e. when replacement of natural habitats occurs and, after that, when urban areas are established and develop in time. It is likely that different factors affect species' ability to cope with these two phases of urbanization, possibly related to both intrinsic species' traits as well as extrinsic landscape configuration, and stochastic processes, thus setting the scene to future research avenues, dealing with species-specific dynamics and responses to urban areas through time.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data are provided in electronic supplementary material [56].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. L.A.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; G.A.: conceptualization, data curation, methodology, validation, writing—original draft; D.C.: conceptualization, data

royalsocietypublishing.org/journal/rspb *Proc. R. Soc. B* **291**: 20240079

Downloaded from https://royalsocietypublishing.org/ on 13 March 2024

curation, investigation; B.C.: conceptualization, investigation, methodology, writing—original draft; M.Z.: conceptualization, data curation, investigation, methodology, validation, writing—original draft; E.M.: conceptualization, formal analysis, investigation, methodology, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. L.A. and E.M. were funded by the National Recovery and Resilience Plan (NRRP), Mission 4, Component 2, Investment 1.4, Decree n.3175 of the Italian Ministry of University and Research, funded by the European Union – NextGenerationEU; Award Number CN_00000033, CUPB83C22002930006, 'National Biodiversity Future Center – NBFC'.

Acknowledgements. We thank three anonymous reviewers whose comments improved the first version of this manuscript. We also thank Andrea Amici, Andrea Monaco and Francesca Manzia for providing essential data for this work.

References

1. Seto KC, Fragkias M, Güneralp B, Reilly MK. 2011 A meta-analysis of global urban land expansion. *PLoS ONE* **6**, e23777. (doi:10.1371/journal.pone.0023777)
2. Sun L, Chen J, Qinglan L, Huang D. 2020 Dramatic uneven urbanization of large cities throughout the world in recent decades. *Nat. Commun.* **11**, 5366. (doi:10.1038/s41467-020-19158-1)
3. Cohen JE. 2003 Human population: the next half century. *Science* **302**, 1172–1175. (doi:10.1126/science.1088665)
4. Huang Q, Liu Z, He C, Gou S, Bai Y, Wang Y, Shen M. 2020 The occupation of cropland by global urban expansion from 1992 to 2016 and its implications. *Environ. Res. Lett.* **15**, 084037. (doi:10.1088/1748-9326/ab858c)
5. Dearborn DC, Kark S. 2010 Motivations for conserving urban biodiversity. *Conserv. Biol.* **24**, 432–440. (doi:10.1111/j.1523-1739.2009.01328.x)
6. Von der Lippe M, Kowarik I. 2008 Do cities export biodiversity? Traffic as dispersal vector across urban–rural gradients. *Div. Distrib.* **14**, 18–25. (doi:10.1111/j.1472-4642.2007.00401.x)
7. Santini L, González-Suárez M, Russo D, Gonzalez-Voyer A, von Hardenberg A, Ancillotto L. 2019 One strategy does not fit all: determinants of urban adaptation in mammals. *Ecol. Lett.* **22**, 365–376. (doi:10.1111/ele.13199)
8. Putman BJ, Tippie ZA. 2020 Big city living: a global meta-analysis reveals positive impact of urbanization on body size in lizards. *Front. Ecol. Evol.* **8**, 580745. (doi:10.3389/fevo.2020.580745)
9. Labadessa R, Ancillotto L. 2023 Small but irreplaceable: the conservation value of landscape remnants for urban plant diversity. *J. Environ. Manage.* **339**, 117907. (doi:10.1016/j.jenvman.2023.117907)
10. Fraissinet M, Ancillotto L, Migliozzi A, Capasso S, Bosso L, Chamberlain DE, Russo D. 2023 Responses of avian assemblages to spatiotemporal landscape dynamics in urban ecosystems. *Landsc. Ecol.* **38**, 293–305. (doi:10.1007/s10980-022-01550-5)
11. Palmero-Iniesta M, Pino J, Pesquer L, Espelta JM. 2021 Recent forest area increase in Europe: expanding and regenerating forests differ in their regional patterns, drivers and productivity trends. *Eur. J. For. Res.* **140**, 793–805. (doi:10.1007/s10342-021-01366-z)
12. Magle SB, Hunt VM, Vernon M, Crooks KR. 2012 Urban wildlife research: past, present, and future. *Biol. Conserv.* **155**, 23–32. (doi:10.1016/j.biocon.2012.06.018)
13. Collins MK, Magle SB, Gallo T. 2021 Global trends in urban wildlife ecology and conservation. *Biol. Conserv.* **261**, 109236. (doi:10.1016/j.biocon.2021.109236)
14. Venditti C, Meade A, Pagel M. 2011 Multiple routes to mammalian diversity. *Nature* **479**, 393–396. (doi:10.1038/nature10516)
15. Loy A, Aloise G, Ancillotto L, Angelici FM, Bertolino S, Capizzi D, Amori G. 2019 Mammals of Italy: an annotated checklist. *Hystrix* **30**, 87–106.
16. Alikhani S, Nummi P, Ojala A. 2021 Urban wetlands: a review on ecological and cultural values. *Water* **13**, 3301. (doi:10.3390/w13223301)
17. Guareschi S, Abellán P, Laini A, Green AJ, Sánchez-Zapata JA, Velasco J, Millán A. 2015 Cross-taxon congruence in wetlands: assessing the value of waterbirds as surrogates of macroinvertebrate biodiversity in Mediterranean Ramsar sites. *Ecol. Indic.* **49**, 204–215. (doi:10.1016/j.ecolind.2014.10.012)
18. Lelo K. 2014 A GIS approach to urban history: Rome in the 18th century. *ISPRS Int. J. Geo-Inf.* **3**, 1293–1316. (doi:10.3390/ijgi3041293)
19. Bianchini L, Egidi G, Alhuseen A, Sateriano A, Cividino S, Clemente M, Imbrenda V. 2021 Toward a dualistic growth? Population increase and land-use change in Rome, Italy. *Land* **10**, 749. (doi:10.3390/land10070749)
20. Fattorini S, Galassi D, Strona G. 2016 When human needs meet beetle preferences: tenebrionid beetle richness covaries with human population on the Mediterranean islands. *Insect Conserv. Divers.* **9**, 369–373. (doi:10.1111/icad.12170)
21. Ancillotto L, Bosso L, Salinas-Ramos VB, Russo D. 2019 The importance of ponds for the conservation of bats in urban landscapes. *Landsc. Urban Plan.* **190**, 103607. (doi:10.1016/j.landurbplan.2019.103607)
22. Di Pietro S, Mantoni C, Fattorini S. 2021 Influence of urbanization on the avian species-area relationship: insights from the breeding birds of Rome. *Urban Ecosyst.* **24**, 779–788. (doi:10.1007/s11252-020-01081-4)
23. Gippoliti S, Amori G. 2006 Historical data on non-volant mammals in Rome: what do they say about urban environment. *Aldrovandia* **2**, 69–72.
24. Amori G, Battisti C, De Felici S. 2009 *I Mammiferi della provincia di roma – dallo stato delle conoscenze alla gestione e conservazione delle specie*. Rome, Italy: Provincia di Roma – Assessorato alle Politiche dell'Agricoltura, Stilgrafica Editions.
25. Gippoliti S. 2009 Contributo alla storia della Teriologia della provincia di Roma. In *Atlante dei mammiferi della provincia di roma-dallo stato delle conoscenze alle strategie di gestione e conservazione* (eds G Amori, C Battisti, S De Felici), pp. 55–58. Stilgrafica, Roma: Provincia di Roma, Assessorato alle Politiche dell'Agricoltura.
26. Zozzoli R, Menchetti M, Mori E. 2018 Spatial behaviour of an overlooked alien squirrel: the case of Siberian chipmunks *Eutamias sibiricus*. *Behav. Processes* **153**, 107–111. (doi:10.1016/j.beproc.2018.05.014)
27. Mori E, Molteni R, Ancillotto L, Ficetola GF, Falaschi M. 2022 Spatial ecology of crested porcupine in a metropolitan landscape. *Urban Ecosyst.* **25**, 1797–1803. (doi:10.1007/s11252-022-01264-1)
28. Miller GS. 1912 *Catalogue of the mammals of Western Europe (Europe exclusive of Russia) in the collection of the British Museum*. London, UK: British Museum.
29. Hoffmann A, Decher J, Rovero F, Schaer J, Voigt C, Wibbelt G. 2010 Field methods and techniques for monitoring mammals. In *Manual on field recording techniques and protocols for all taxa biodiversity inventories* (eds J Eymann, J Degreef, C Häuser, JC Monje, Y Samyn, D VandenSpiegel), pp. 482–529. London, UK: ABC Taxa Editions.
30. R Core Team. 2023 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org/.
31. Bates D *et al*. 2009 Package 'lme4'. See http://lme4.r-forge.r-project.org.
32. Hartig F, Hartig MF. 2017 Package 'DHARMa'. R package. See https://cran.r-hub.io/web/packages/DHARMa/DHARMa.pdf.

33. Barton K. 2009 MuMIn: multi-model inference. R package version 1.0.0. See http://r-forge.r-project.org/projects/mumin/.
34. Adams LW. 1994 *Urban wildlife habitats: a landscape perspective*, vol. 3. Minneapolis, MN: University of Minnesota Press.
35. Reis V, Hermoso V, Hamilton SK, Ward D, Fluet-Chouinard E, Lehner B, Linke S. 2017 A global assessment of inland wetland conservation status. *Bioscience* **67**, 523–533. (doi:10.1093/biosci/bix045)
36. Kingsford RT, Basset A, Jackson L. 2016 Wetlands: conservation's poor cousins. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* **26**, 892–916. (doi:10.1002/aqc.2709)
37. Serra-Cobo J, Lopez-Roig M, Marques-Bonet T, Lahuerta E. 2000 Rivers as possible landmarks in the orientation flight of *Miniopterus schreibersii*. *Acta Theriologica* **45**, 347–352. (doi:10.4098/AT.arch.00-34)
38. Almenar D, Aihartza J, Goiti U, Salsamendi E, Garin I. 2009 Foraging behaviour of the long-fingered bat *Myotis capaccinii*: implications for conservation and management. *Endang. Species Res.* **8**, 69–78. (doi:10.3354/esr00183)
39. Solimini AG, Gulia P, Monfrinotti M, Carchini G. 2000 Performance of different biotic indices and sampling methods in assessing water quality in the lowland stretch of the Tiber River. *Hydrobiologia* **422**, 197–208. (doi:10.1023/A:1017090804460)
40. Testi A, Bisceglie S, Guidotti S, Fanelli G. 2009 Detecting river environmental quality through plant and macroinvertebrate bioindicators in the Aniene River (Central Italy). *Aquat. Ecol.* **43**, 477–486. (doi:10.1007/s10452-008-9205-8)
41. Battisti C, Amori G, Luiselli L, Angelici FM, Zapparoli M. 2011 Can the grey literature help us understand the decline and extinction of the near threatened Eurasian otter *Lutra lutra* in Latium, central Italy? *Oryx* **45**, 281–287. (doi:10.1017/S0030605310001055)
42. Shanahan DF, Strohbach MW, Warren PS, Fuller RA. 2014 The challenges of urban living. In *Avian urban ecology: behavioural and physiological adaptations* (eds D Gill, H Brumm), pp. 3–20. Oxford, UK: Oxford University Press.
43. Jones G, Barratt EM. 1999 *Vespertilio pipistrellus* Schreber, 1774 and *V. pygmaeus* Leach, 1825 (currently *Pipistrellus pipistrellus* and *P. pygmaeus*; Mammalia, Chiroptera): proposed designation of neotypes. *Bull. Zool. Nomencl.* **56**, 182–186.
44. Razgour O *et al*. 2013 *Conserving grey long-eared bats (Plecotus austriacus) in our landscape: a conservation management plan*. London, UK: Bat Conservation Trust.
45. von Thaden A, Büchner S, Lang J, Meinig H, Nowak C. 2022 Combining citizen science and conservation genomics to reveal the causes of rapid population decline in the garden dormouse (*Eliomys quercinus*). In ARPHA Conference Abstracts, *vol. 5*, e84437. Pensoft Publishers.
46. Mori E, Sangiovanni G, Corlatti L. 2020 Gimme shelter: the effect of rocks and moonlight on occupancy and activity pattern of an endangered rodent, the garden dormouse *Eliomys quercinus*. *Behav. Processes* **170**, 103999. (doi:10.1016/j.beproc.2019.103999)
47. Lowry H, Lill A, Wong BB. 2013 Behavioural responses of wildlife to urban environments. *Biol. Rev.* **88**, 537–549. (doi:10.1111/brv.12012)
48. Bonier F, Martin PR, Wingfield JC. 2007 Urban birds have broader environmental tolerance. *Biol. Lett.* **3**, 670–673. (doi:10.1098/rsbl.2007.0349)
49. MacGregor-Fors I, García-Arroyo M, Quesada J. 2022 Keys to the city: an integrative conceptual framework on avian urban filtering. *J. Urban Ecol.* **8**, juac026.
50. Croci S, Butet A, Clergeau P. 2008 Does urbanization filter birds on the basis of their biological traits. *Condor* **110**, 223–240. (doi:10.1525/cond.2008.8409)
51. Callaghan CT, Major RE, Wilshire JH, Martin JM, Kingsford RT, Cornwell WK. 2019 Generalists are the most urban-tolerant of birds: a phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos* **128**, 845–858. (doi:10.1111/oik.06158)
52. Luniak M. 2008 Fauna of the big city – estimating species richness and abundance in Warsaw, Poland. In *Urban ecology* (eds JM Marlzuff, E Shulenberger, W Endlicher, M Alberti, G Bradley, C Ryan, U Simon, C ZumBrunnen), pp. 349–354. Boston, MA: Springer US.
53. Fattorini S. 2014 Urban biodiversity hotspots are not related to the structure of green spaces: a case study of tenebrionid beetles from Rome, Italy. *Urban Ecosyst.* **17**, 1033–1045. (doi:10.1007/s11252-014-0375-y)
54. Rodewald AD, Gehrt SD. 2014 Wildlife population dynamics in urban landscapes. In *Urban wildlife conservation: theory and practice* (eds RA McCleery, CE Moorman, MN Peterson), pp. 117–147. Boston, MA: Springer.
55. Boakes Z, Stafford R, Bramer I, Cvitanović M, Hardouin EA. 2023 The importance of urban areas in supporting vulnerable and endangered mammals. *Urban Ecosyst.* **2023**, 1–12. (doi:10.1007/s11252-023-01492-z)
56. Ancillotto L, Amori G, Capizzi D, Cignini B, Zapparoli M, Mori E. 2024 No city for wetland species: habitat associations affect mammal persistence in urban areas. Figshare. (doi:10.6084/m9.figshare.c.7099106)

Downloaded from https://royalsocietypublishing.org/ on 13 March 2024